

Variability and distribution of *Pluteus luteus*, a later synonym of *P. variabilicolor*

HANA ŠEVČÍKOVÁ^{1*} & BÁLINT DIMA²

^{1*} Department of Botany, Moravian Museum,
Zelný trh 6, CZ-659 37 Brno, Czech Republic

² Department of Plant Anatomy, Institute of Biology, Eötvös Loránd University,
Pázmány Péter sétány 1/c, H-1117 Budapest, Hungary

* CORRESPONDENCE TO: hsevcikova@mzm.cz

ABSTRACT—The type specimen of *Pluteus luteus* was studied morphologically and molecularly using DNA sequences of the ITS region of the ribosomal RNA gene. *Pluteus luteus* is reduced to a synonym of *P. variabilicolor*, the morphological variability of which is discussed. The distribution of *P. variabilicolor* as a species native to Europe and Asia is summarized, including the first collection from Slovakia and the second report from the Republic of Korea (South Korea).

KEY WORDS—Agaricales, Pluteaceae, *Pluteus* sect. *Hispidoderma*, type studies, taxonomy

Introduction

Pluteus Fr. (Agaricales, Pluteaceae; Kotlaba & Pouzar 1972, Singer 1986, Justo & al. 2011a) is characterized by free lamellae, a pinkish spore print, smooth globose to ellipsoid (rarely oblong) basidiospores, an inverse hymenophoral trama, and the presence of cheilocystidia, often also pleurocystidia (Singer 1986, Vellinga 1990).

Traditionally, three sections are distinguished in the genus: *Pluteus* sect. *Pluteus*; *P.* sect. *Hispidoderma* Fayod; and *P.* sect. *Celluloderma* Fayod, divided into *P.* subsect. *Eucellulodermini* Singer and *P.* subsect. *Mixtini* Singer (Singer 1986). *Pluteus* sect. *Pluteus* is characterized by a pileipellis in the form of a cutis and thick-walled pleurocystidia with hooks, prongs or other types of excrescences; *P.* sect. *Hispidoderma* by a pileipellis consisting of elongated,

filiform or hyphal elements organized as a cutis, a hymeniderm or a trichoderm, and with non-metuloid pleurocystidia; and *P. sect. Celluloderma* by a pileipellis composed of relatively short (sphaeropedunculate, ellipsoid to saccate-obpyriform) elements organized with (*P. subsect. Mixtini*) or without (*P. subsect. Eucellulodermini*) longer elements, which may be interpreted as dermatocystidia or pileocystidia, as a hymeniderm, and non-metuloid pleurocystidia (Singer 1956, 1958, 1986; Orton 1986, Citérin & Eyssartier 1998). According to Justo & al. (2011a,b), these subsections are not natural groups, because elongated elements have appeared several times during the evolution of *P. sect. Celluloderma* and also some species with a cutis pileipellis (e.g., *P. fenzi* (Schulzer) Corriol & P.-A. Moreau) are members of this section. Babos (1978) originally assigned *Pluteus variabilicolor* Babos to *P. subsect. Mixtini*. However, our phylogenetic analysis of nrDNA ITS sequences, in accordance with previous articles (Justo & al. 2011a, Lezzi & al. 2014), shows that it belongs to *P. sect. Hispidoderma*, together with *P. leoninus* (Schaeff.) P. Kumm. The explanation of this discrepancy is provided in this paper, based on micromorphological and phylogenetical studies.

Pluteus variabilicolor was described based on collections from Hungary, but the author pointed out that most of the species of *P. subsect. Mixtini* are non-European (Babos 1978). Later, *Pluteus castroae* Justo & E.F. Malysheva [as “*castr*”] described from Russia and Japan (Justo & al. 2011a: 470) was synonymized with *Pluteus variabilicolor* (Lezzi & al. 2014). *Pluteus luteus* was originally described as *Macrocystidia lutea* from China (Redhead & Liu 1982), but the authors stated *M. lutea* to be an anomalous species in *Macrocystidia* and after two years, Redhead (1984) transferred it to *Pluteus*.

In this paper, *Pluteus luteus* is reduced to a synonym under *P. variabilicolor*. The distribution of this species in Europe and Asia is summarized including the first collections from Slovakia and the second report from the Republic of Korea.

Materials & methods

Morphology

Macroscopic descriptions of the collected specimens are based on fresh basidiomata. Microscopic features were studied on dried material mounted in Congo red using an Olympus BX-50 light microscope at magnifications of 400× and 1000×. Herbarium abbreviations are according to Thiers (2019). Morphological terminology follows Vellinga (1988). Authors of fungal names are cited according to the Index Fungorum Authors of Fungal Names website (<http://www.indexfungorum.org/names/AuthorsOfFungalNames.asp>). Abbreviations: avl = mean of basidiospore length;

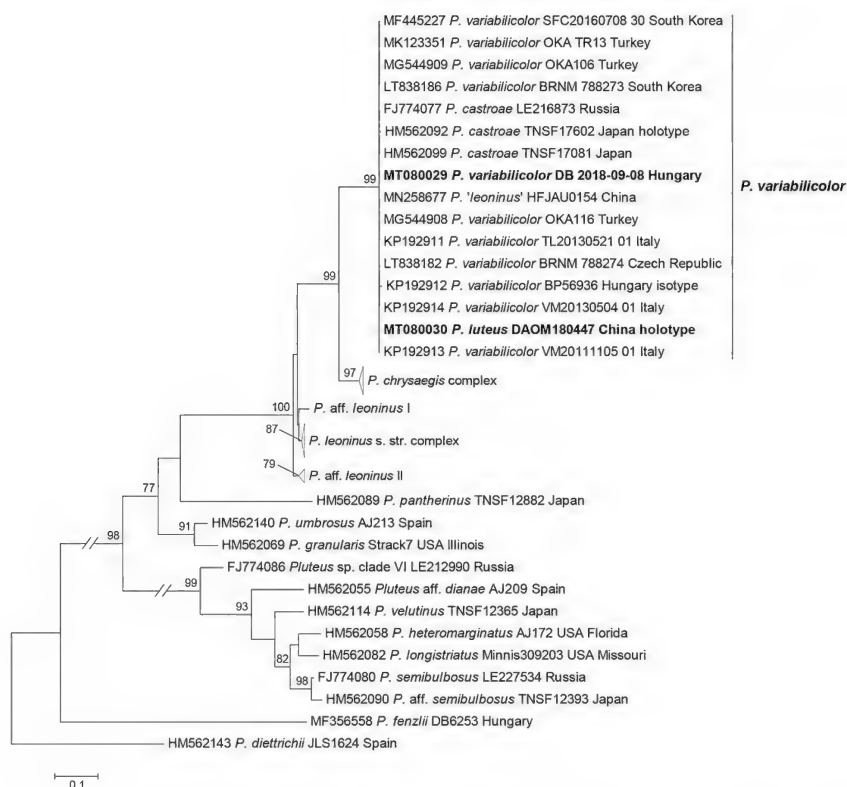


Fig. 1. Maximum likelihood phylogenetic tree inferred from nrDNA ITS data set, showing the relationships in *Pluteus* sect. *Hispidoderma*. Species complexes not dealt with in this study are shown as compressed clades. Newly generated sequences are highlighted in bold. PhyML bootstrap support values are shown at the branches. Bar indicates 0.1 expected change per site per branch.

avw = mean of basidiospore width; Q = quotient of length and width in any one basidiospore; avQ = mean of basidiospore Q-values.

Molecular phylogeny

For DNA extraction, only dried herbarium specimens were used. DNA was extracted with the NucleoSpin Plant II Mini Kit. PCR amplification of the internal transcribed spacer region (ITS) of the ribosomal RNA gene was performed with the primer pair ITS1F/ITS4 (White & al. 1990, Gardes & Bruns 1993). Sequencing of the amplicons was carried out with the same primers by LGC Genomics (Berlin, Germany). Chromatograms were checked and assembled with CodonCode Aligner 8.0.1. Initial BLAST search in the GenBank and UNITE nucleotide databases was performed to find homologous sequences. ITS sequences of *Pluteus* belonging to

P. sect. Hispidoderma were downloaded based on previous studies (e.g. Justo & al. 2011a, Lezzi & al. 2014). The names of HM562055 (*Pluteus* aff. *dianae*) and FJ774086 (*Pluteus* sp. clade VI) follow a previous taxonomic paper (Ševčíková & al. 2020). Sequences were aligned with the online version of MAFFT v. 7 using the E-INS-i algorithm (Katoh & Standley 2013). Alignment was inspected and edited with SeaView 4 (Gouy & al. 2010).

Maximum Likelihood analysis was performed in PhyML 3.1 (Guindon & Gascuel 2003) using the GTR+I+G model of evolution and gamma distribution of 8 rate categories. The resulting tree was edited in MEGA 7 (Kumar & al. 2016).

Phylogenetic results

The aligned ITS data set comprised a total of 40 sequences and a length of 700 positions including gaps which were treated as missing data in the ML analysis. Two new sequences were deposited in GenBank (MT080029 and MT080030). The resulting phylogram is shown in Fig. 1. Based on our analysis, the ITS sequence generated from the holotype of *Pluteus luteus* nests within the same clade including the holotype sequences of *Pluteus variabilicolor* and *P. castroae*, with high support (ML-BS = 99%). This clade forms a sister group of the *Pluteus chrysaeigis* complex, as shown in Lezzi & al. (2014).

Taxonomy

Pluteus variabilicolor Babos,

Annales Historico-Natureles Musei Nationalis Hungarici 70: 93 (1978) FIG. 2, 4

= *Macrocyttidia lutea* Redhead & B. Liu, Canadian Journal of Botany 60(8): 1485 (1982)

= *Pluteus luteus* (Redhead & B. Liu) Redhead, Sydowia 37: 266 (1984)

= *Pluteus castroae* Justo & E.F. Malysheva [as '*castri*'], in Justo & al.,

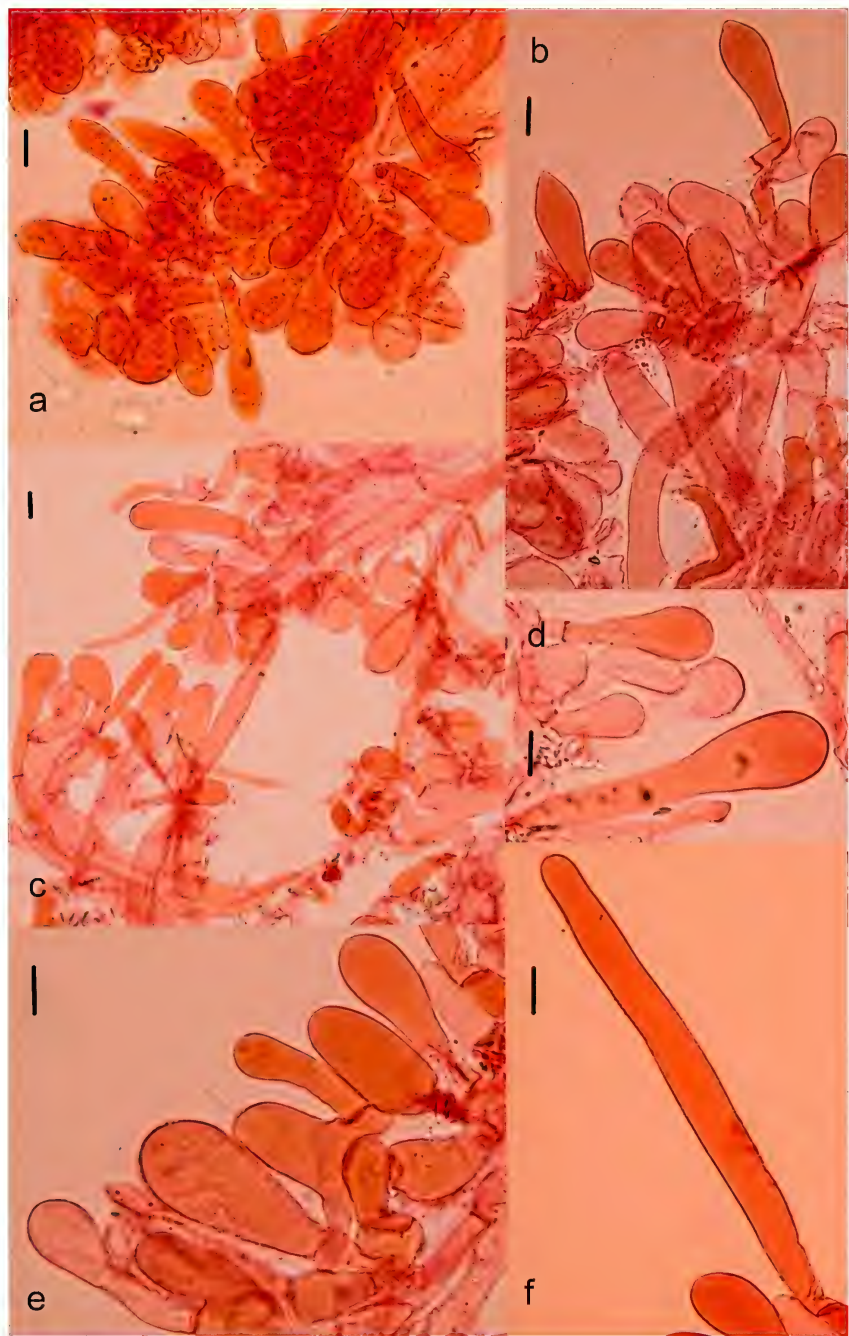
Mycological Progress 10(4): 470 (2011)

Type revision of *Pluteus luteus*

FIGS 2a, e–f; 3

ORIGINAL DESCRIPTION OF *MACROCYTTIDIA LUTEA* — “Pileus 5–14 mm lat., campanulatus ad convexus umbone, humidus, translucidus, glabratus, levis, luteus, in sicco infuscato. Lamellae adnatae, ascendens, latae, confertae, albae, in siccis salmoneis. Stipes 12–60 × 1–1.3 mm, levis, albus, in sicco ochraceo. Basidiosporae 5–6 × 4–5.8 µm, subglobose, angulatus obscure, subhyalinae ad subsalmoneus, inamyloideae, leves, cyanophilae praecipue. Basidia tetraspora, clavata. Cheilocystidia et pleurocystidia 42–57 × 11–22 µm, dispersa, fusiformia ad ventricosa, levia. Pileocystidia abundant, clavata ad ventricosa, levia, implexa, 28–52 × 11–14 µm. Caulocystidia apiceum versus, aggregata, clavata ut mucronata interdum. Hyphae fibulis nullis. *Lactocollybia* affinis.”

Fig. 2. *Pluteus variabilicolor*, pileipellis elements. a. DAOM 180447, holotype of *P. luteus*, young basidioma; b. BRNM 788274; c. BRNM 772177; d. BRNM 788273; e, f. DAOM 180447, holotype of *P. luteus*, mature basidioma. Scale bars = 10 µm.



HOLOTYPE—China, Kiangsu Province, Nanking City, June 27, 1978, Liu Bo 432, on rotting wood in mountains (DAOM 180447).

BASIDIOSPORES $5\text{--}6.5(-7.5) \times (4\text{--})4.5\text{--}6\ \mu\text{m}$, $avl \times avw = 5.9 \times 5.1\ \mu\text{m}$, $Q = 1.00\text{--}1.40$, $avQ = 1.16$, subglobose, rarely broadly ellipsoid or globose with small inconspicuous apices. BASIDIA $20\text{--}31(-33) \times 6\text{--}8(-11)\ \mu\text{m}$, tetrasterigmate, clavate to subfusiform or narrowly utriform, colourless. PLEUROCYSTIDIA abundant, $40\text{--}51.5(-78) \times 11\text{--}19(-24)\ \mu\text{m}$, clavate to broadly clavate, with obtuse or slightly acuminate apex, narrowly to broadly fusiform, less frequently narrowly lageniform or narrowly utriform, with obtuse apex or rarely with small rostrate apex, hyaline, thin-walled. Lamellar edges sterile. CHELOCYSTIDIA $(22\text{--})31\text{--}52 \times (7\text{--})10.5\text{--}22\ \mu\text{m}$, narrowly to broadly fusiform, with obtuse apex or rarely with $1\text{--}4\ \mu\text{m}$ long rostrate apex, or clavate to broadly clavate, with obtuse or slightly acuminate apex, less frequently narrowly lageniform or narrowly utriform, very rarely with $1\text{--}3\ \mu\text{m}$ long rostrate apex, hyaline, thin-walled. PILEIPELLIS a euhymeniderm composed of two types of elements: [1] $(17\text{--})20\text{--}54(-57) \times 11\text{--}17(-19.5)\ \mu\text{m}$, narrowly clavate to clavate, narrowly fusiform to fusiform, frequently with obtuse apex or $1\text{--}4\ \mu\text{m}$ long (sub)rostrate apex; [2] $(120\text{--})181\text{--}210(-220) \times 8\text{--}16\ \mu\text{m}$ elongate (sub)cylindrical elements with obtuse apex; both types with yellow or pale yellow-ochre intracellular pigment, less frequently almost colourless with very pale yellow tinge, thin-walled. STIPITPELLIS a cutis of $4\text{--}12(-16)\ \mu\text{m}$ diam cylindrical thin-walled, colourless or pale ochre-coloured hyphae. CAULOCYSTIDIA in tufts, more frequently in lower part of stipe, $14\text{--}30(-42) \times 4\text{--}11(-19.5)\ \mu\text{m}$, subcylindrical, narrowly clavate to broadly clavate, fusiform or utriform, often with $1\text{--}4\ \mu\text{m}$ long rostrate apex, thin-walled, colourless, in lower part of mature basidioma with brown intracellular pigment. CLAMP CONNECTIONS absent from all tissues.

Distribution and ecology

So far *Pluteus variabilicolor* is known from Europe: Hungary (Babos 1978), Austria (Lohmeyer & al. 1994), Italy (Lanconelli & al. 1998, Migliozi 2011, Lezzi & al. 2014), Spain (Sánchez & Muñoz 2018), Romania (BRA 32267, Béres 2012), Slovenia and Moldova (Lezzi & al. 2014), and Russia (Justo & al. 2011a) – and from Asia: Japan (Justo & al. 2011a), China (as *P. luteus*; Redhead & Liu 1982, Redhead 1984), and the Republic of Korea (as *P. luteus*; Lee & al. 2016). A second collection from the Republic of Korea is reported from a dead trunk of *Castanea* in a mixed forest (BRNM 788273). *Pluteus variabilicolor* was found for the first time in Slovakia at two localities, one on a heap of sawdust and the other on decayed wood of a deciduous tree in a deciduous forest (BRNM 788274, BRNM 772177). This species is probably widespread but rare in

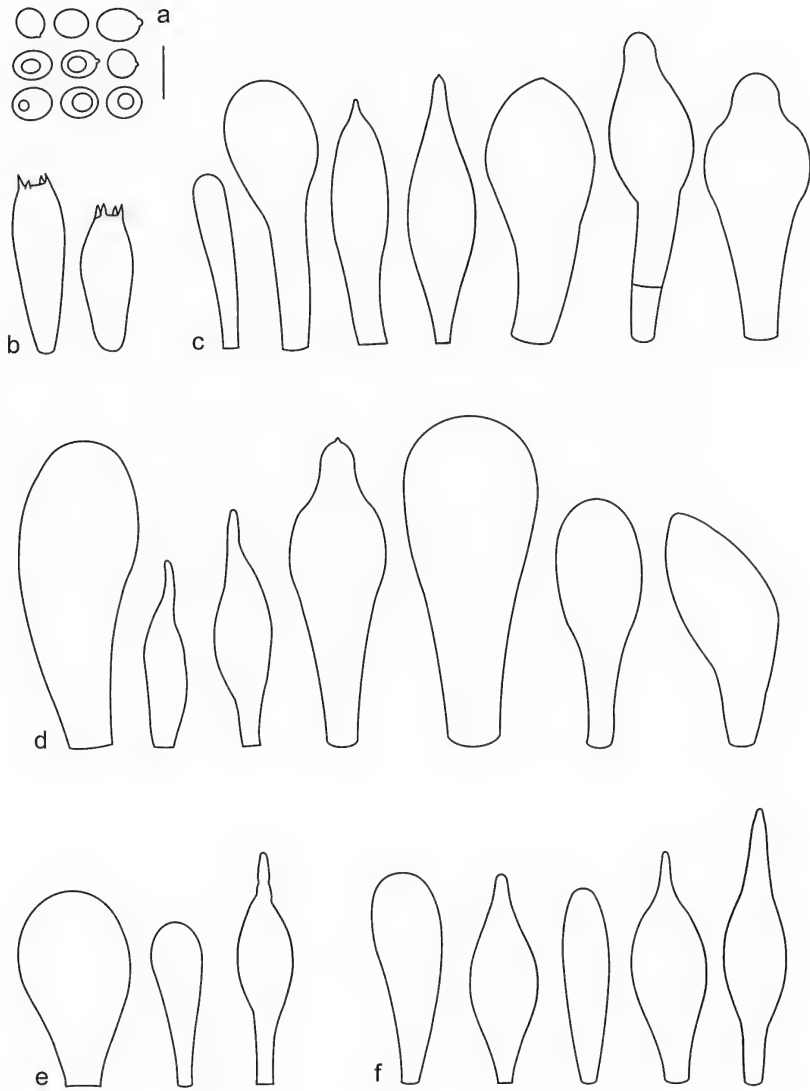


Fig. 3. *Pluteus luteus* (holotype, DAOM 180447). a. basidiospores; b. basidia; c. cheilocystidia; d. pleurocystidia; e. caulocystidia of young basidioma; f. caulocystidia of mature basidioma. Scale bar = 10 μ m.

Europe and Asia, growing on decayed wood (mostly fallen trunks), sawdust, or woodchips of deciduous trees from May to October (BRNM 772177, BRNM 788273, BRNM 788274, Babos 1978, Béres 2012, Justo & al. 2011a, Lanconelli & al. 1998, Lezzi & al. 2014, Lohmeyer & al. 1994, Migliozi 2011, Redhead & Liu 1982, Redhead 1984, Sánchez & Muñoz 2018).

Discussion

Phylogenetically, the lineage of *Pluteus variabilicolor* [= *P. luteus*; = *P. castroae*] forms a uniform and isolated clade, supported by our ML analysis of the ITS dataset. The sequence variation among the specimens studied was low: 1–6 substitution or indel positions. However, most of these variations originated from polymorphic sites and might not be real differences. (These sequences contain uncertain positions, where base polymorphisms occur, marked with IUB codes. Therefore, these cannot be counted as real differences with certainty.) The closest sister taxon, the *P. chrysaegis* complex, differs by more than 50 substitution and indel positions.

Pluteus luteus was originally described as *Macrocystidia lutea*. Redhead & Liu (1982) mentioned ascending adnate lamellae, whereas the genus *Pluteus* is characteristic by free lamellae. Redhead (1984), who had never seen fresh material, later revised the description from the type collection and combined the name with *Pluteus* to draw attention to the original misclassification. Redhead based the reclassification upon the convergent pluteoid tramal structure and a more palisade-like nature of the pileipellis on the disc but did not mention the attachment of the lamellae. The type material contains one larger and several small young basidiomata on which the lamellar attachment is not clear. After cutting the basidioma, we observed that the lamellae appear to be free.

Pluteus variabilicolor is, as its name implies, a variable species. Babos (1978) mentioned a white (or yellowish) stipe with dark floccules (as in *Leccinum*), sometimes only on the basal part of the stipe or as inconspicuous floccules visible only with a lens. Liu described *Pluteus luteus* as having a white stipe when fresh, turning ochraceous on drying (Redhead & Liu 1982). In our type studies (DAOM 180447!), we found only rare tufts of brownish caulocystidia in the lower part of the stipe of a mature basidioma and scattered colourless caulocystidia in the upper part. Therefore, the dark floccules on the stipe are not a significant feature for identification of *P. variabilicolor*. Moreover, the stipes of the Slovakian collection BRNM 788274 (relatively young basidiomata) have yellow-ochre to mustard yellow fibrils on a white background, and brown on white background in the lower part, at least at the stipe base (see FIG. 4).



Fig. 4. *Pluteus variabilicolor*, basidiomata. a–c. BRNM 788274 (photo J. Pavlík); d. BRNM 788273 (photo V. Antonín); e. BRNM 772177 (photo J. Hraško); f. BRNM 817743 (photo D. Solár).

Babos (1978) cited various pileus colours for the young basidiomata: lemon-, chrome- or orange-yellow, sometimes with mustard to brownish green tinges, paler at the pileus margin, and brown or grey-brown fibrillose scales.

The Slovak and South Korean collections (BRNM 788274; BRNM 772177; BRNM 788273; see FIG. 4) confirm this variability.

Lezzi & al. (2014) mentioned a difference in the pileipellis structure between the original description of *P. variabilicolor* and the Italian collections identified originally as *P. castroae*; phylogenetically they were identical and synonymized under *P. variabilicolor*. According to Lezzi & al. (2014), Italian collections lack the elongated pileipellis elements (up to 200 µm long) found in collections of *P. variabilicolor*. Our holotype studies show that elongate elements of up to 210 µm are frequent in mature basidiomata (BP85860, isotype of *P. variabilicolor*; large basidioma labelled as the holotype of *P. luteus*, DAOM 180447; also BRNM 788274, etc.). Shorter elements dominate in young basidiomata (BRNM 788273; small basidiomata of DAOM 180447, etc.); elongate elements are very rare and inconspicuous and thus may, in some cases, look like subpellis elements. The long elements also prevail at the pileus margin. In some cases, long elements are absent at least in middle parts of the pileus of very young basidiomata (the smallest basidioma of DAOM 180447; LE 212090).

Pluteus variabilicolor was initially included within *P.* subsect. *Mixtini* (Babos 1978) but belongs phylogenetically to *P.* sect. *Hispiderma* (Justo & al. 2011a, Lezzi & al. 2014, our studies – see FIG. 1). Moreover, our morphological studies of the type show that the pileipellis structure of *P.* subsect. *Mixtini* within the traditional *P.* sect. *Celluloderma* differs significantly from the pileipellis structure of species belonging phylogenetically to *P.* sect. *Hispiderma*. Singer (1986) pointed out that the pileipellis of *P.* subsect. *Mixtini* is based on short (ellipsoid to saccate-obpyriform) elements, and elongate elements can be interpreted as dermatocystidia (= pileocystidia). By contrast, a pileipellis formed of long elements is typical of species belonging to *P.* sect. *Hispiderma*. Thus, the long elements of *P. variabilicolor* probably form the pileipellis as well as the shorter elements. Our morphological studies show that the long elements grow later during basidioma ontogenesis, which is a very unusual phenomenon in *Pluteus*. Further investigation of the growth dynamics of the pileipellis is needed.

Babos (1978) and Courtecuisse (2006) mentioned *Pluteus variabilicolor* as possibly introduced into Europe. The new records from Slovakia and South Korea confirm that this species is widespread in Eurasia and supports the theory that *P. variabilicolor* is a native species in the temperate zone of Europe and Asia.

COLLECTIONS STUDIED—*Pluteus variabilicolor*: HUNGARY. Prope Szárliget, in heap of sawdust, 6 July 1977, leg. M. Babos et A. Friesz, det. M. Babos (BP85860 isotype); 19 Aug. 1974, leg. E. Véssey, det. M. Babos (BP56982); Budai Mts, Mt. Jánoshegy, on rotten trunk, 19 June 1960, leg. I. Szőke, det. M. Babos (BP34357); Visegrádi Mts, Dömös, Malom-patak, in heap of sawdust, 23 July 1968, leg. et det. M. Babos (BP47697); Solymár, in heap of sawdust, 3 Sept. 1977, leg. K. Tallér, det. M. Babos (BP56990). AUSTRIA. Tittmining-Ettenau, heap of bark mulch (*Populus?*), 30 Oct. 1993, leg. R. Till et T.R. Lohmeyer, det. H. Forstinger (L 7942/2). ROMANIA. Moraresti, near Lintesti, decaying sawdust of *Quercus*, 3 June 1979 leg. et det. J. Kuthan (BRA 32267). SLOVAKIA. Snina, Hrb, heap of sawdust, 10 May 2010, leg. J. Pavlík, det. H. Ševčíková (BRNM 788274); Mládzo, Hlonča, deciduous forest, on decayed wood of deciduous tree, 21 Oct. 2015, leg. J. Hraško, det. H. Ševčíková (BRNM 772177); Lošonec, Lošonský háj, on trunk of *Quercus*, 13 September 2019 leg. D. Solár, det. H. Ševčíková (BRNM 817743). REPUBLIC OF KOREA. Taean Peninsula, Deoksung, Sudeoksa Monastery, mixed forest, dead trunk of *Castanea*, 7 Aug. 2014, leg. V. Antonín, det. H. Ševčíková (BRNM 788273).

Pluteus variabilicolor [originally as *P. castroae*]: RUSSIA. Samara Region, near Pribezny, on decaying wood of deciduous tree, 1 July 2007, leg. et det. E.F. Malysheva (LE 212090, paratype).

Pluteus variabilicolor [originally as *P. luteus*]: CHINA. Kiangsu Province, Nanking City, on rotting wood in mountains, 27 June 1978, leg. B. Liu (DAOM 180447, holotype).

Pluteus fenzlii [originally as *P. variabilicolor*]: HUNGARY. Vas, Hosszúpereszteg, on heap of sawdust, 7 Oct. 1990, leg. P. Serediuk, det. J. Borovička (BP 88763).

Conclusions

According to our results, *Pluteus luteus* (as well as *P. castroae*) is a synonym of *P. variabilicolor* and belongs to *P. sect. Hispidoderma*. This taxon is macroscopically and microscopically variable in colour and in structure of pileus and stipe. The most significant characters of *P. variabilicolor* are its yellow to ochre pileus, mostly clavate or fusiform thin-walled pleurocystidia and cheilocystidia often with an obtuse apex or rostrum. Pileipellis structure is also important for distinguishing *P. variabilicolor* from other species, but this character changes during the growth of the basidiomata. The shorter elements prevail over the long elements in the pileipellis of very young basidiomata in our studied collections. With aging basidiomata, however, this ratio significantly changes even in one population. A stipe with conspicuous dark floccules on a white ground is not a stable character. The stipe may also be white without conspicuous floccules; the lower part of the stipe may also have a yellow colour. *Pluteus variabilicolor* is rare but widespread in Europe and Asia on decayed wood, sawdust, or woodchips of deciduous trees. Its distribution indicates it is native to temperate Eurasia.

Acknowledgements

The authors thank S.A. Redhead (Ottawa Research and Development Centre, Agriculture & Agri-food Canada) and E.F. Malysheva (Komarov Botanical Institute of the Russian Academy of Sciences, Saint Petersburg) for their pre-submission reviews of the manuscript and S.R. Pennycook for his nomenclatural review. The authors thank curators of BP, BRA, DAOM, LE and L for the possibility to study herbarium collections. V. Antonín, J. Hraško, J. Pavlík, and D. Solár are acknowledged for providing information about their collections and photos of basidiomata in situ. We also thank S.A. Redhead and E.F. Malysheva for giving useful details of the holotype collection of *Pluteus luteus* and *P. castroae*. We also thank J.W. Jongepier who helped improve the overall language of the manuscript. The studies of the first author were enabled by support provided to the Moravian Museum by the Ministry of Culture of the Czech Republic as part of its long-term conceptual development programme for research institutions (DKRVO, ref. MK000094862). The studies of the second author were partly supported by the ELTE Institutional Excellence Program financed by the National Research, Development and Innovation Office (NKFIH-1157-8/2019-DT).

Literature cited

- Babos MG. 1978. *Pluteus* studies, I. (*Basidiomycetes*, *Pluteaceae*). *Annales Historico-Natureles Musei Nationalis Hungarici* 70: 93–97.
- Béres M. 2012. Macromycetes species included in Bern Convention Appendix in the Red List for Romania, and rare presence in historical Maramures area (Romania). *Acta Oecologica Carpatica* 5: 19–38.
- Citérin M, Eyssartier G. 1998. Clé analytique du genre *Pluteus* Fr. *Documents Mycologiques* 28(111): 47–67.
- Courtecuisse R. 2006. La notion d'espèce invasive appliquée aux champignons – état des lieux, en particulier en France. *La Lettre de la Société Mycologique de France* 8: 5–8.
- Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2(2): 113–118. <https://doi.org/10.1111/j.1365-294X.1993.tb00005.x>
- Gouy M, Guindon S, Gascuel O. 2010. SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* 27: 221–224. <https://doi.org/10.1093/molbev/msp259>
- Guindon S, Gascuel O. 2003. A simple, fast and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52(5): 696–704. <https://doi.org/10.1080/10635150390235520>
- Justo A, Minnis AM, Ghignone S, Menolli N, Capelari M, Rodríguez O, Malysheva E, Contu M, Vizzini A. 2011a. Species recognition in *Pluteus* and *Volvopluteus* (*Pluteaceae*, *Agaricales*): morphology, geography and phylogeny. *Mycological Progress* 10(4): 453–479. <https://doi.org/10.1007/s11557-010-0716-z>
- Justo A, Vizzini A, Minnis AM, Menolli Jr N, Capelari M, Rodríguez O, Malysheva E, Contu M, Ghignone S, Hibbett DS. 2011b. Phylogeny of the *Pluteaceae* (*Agaricales*, *Basidiomycota*): taxonomy and character evolution. *Fungal Biology* 115(1): 1–20. <https://doi.org/10.1016/j.funbio.2010.09.012>

- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kotlaba F, Pouzar Z. 1972. Taxonomic and nomenclatural notes on some macromycetes. *Česká Mykologie* 26(4): 217–222.
- Kumar S, Stecher G, Tamura K. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33(7): 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Lanconelli L, Ballanti F, Rava M. 1998. *Funghi del Lughese*. Faenza: Edit. Faenza.
- Lezzi T, Vizzini A, Ercole E, Migliozi V, Justo A. 2014. Phylogenetic and morphological comparison of *Pluteus variabilicolor* and *P. castri* (Basidiomycota, Agaricales). *IMA Fungus* 5(2): 415–423. <https://doi.org/10.5598/imafungus.2014.05.02.06>
- Lee JS, Choi SY, Kim C, Lee HB. 2016. Twelve undescribed species of macrofungi from Korea. *Korean Journal of Mycology* 44(4): 233–239. <https://doi.org/10.4489/KJM.2016.44.4.233>
- Lohmeyer TR, Christian J, Gruber O. 1994. Ein Nachweis von *Pluteus variabilicolor* in Oberösterreich. *Österreichische Zeitschrift für Pilzkunde* 3: 95–100.
- Migliozi V. 2011. *Pluteus variabilicolor*, specie frequente nella cerreta di Macchiagrande di Manziana (RM). *Parliamo di Funghi* 19(1): 3–9.
- Orton PD. 1986. *British fungus flora: agarics and boleti*. Vol. 4. *Pluteaceae: Pluteus & Volvariella*. Royal Botanic Garden Edinburgh.
- Redhead SA. 1984. Mycological observations, 4–12: on *Kuehneromyces*, *Stropharia*, *Marasmius*, *Mycena*, *Geopetalum*, *Omphalopsis*, *Phaeomarasmius*, *Naucoria* and *Prunulus*. *Sydowia* 37: 246–270.
- Redhead SA, Liu B. 1982. New species and new records of *Tricholomataceae* (Agaricales) from China. *Canadian Journal of Botany* 60(8): 1479–1486. <https://doi.org/10.1139/b82-189>
- Singer R. 1956. Contributions towards a monograph of the genus *Pluteus*. *Transactions of the British Mycological Society* 39: 145–232. [https://doi.org/10.1016/s0007-1536\(56\)80001-6](https://doi.org/10.1016/s0007-1536(56)80001-6)
- Singer R. 1958. Monographs of South American *Basidiomycetes*, especially those of the east slope of the Andes and Brazil 1. The genus *Pluteus* in South America. *Lloydia* 21: 195–299.
- Singer R. 1986. *The Agaricales in modern taxonomy*. 4th edn. Koeltz Scientific Books, Koenigstein.
- Sánchez L, Muñoz G. 2018. *Pluteus variabilicolor* Babos, primera cita para la Península Ibérica. *Revista Catalana de Micologia* 39: 111–116.
- Ševčíková H, Malysheva E, Justo A, Heilmann-Clausen J, Tomšovský M. 2020. *Pluteus diana* and *Pluteus punctatus* resurrected, with first records from eastern and northern Europe. *Mycotaxon* 135(2): 245–274. <https://doi.org/10.5248/135.245>
- Thiers B. 2019 [continuously updated]. Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. [Accessed 24 January 2019: <http://sweetgum.nybg.org/ih/>].
- Vellinga EC. 1988. Glossary. 54–64, in: C Bas & al. (eds). *Flora Agaricina Neerlandica*, vol. 1. Rotterdam.
- Vellinga EC. 1990. *Pluteaceae* Kotl. & P. 31–55, in: C Bas & al. (eds). *Flora Agaricina Neerlandica*, vol. 2. Rotterdam.
- White TJ, Bruns T, Lee S, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. 315–322, in: MA Innis & al. (eds). *PCR protocols: a guide to methods and applications*. New York: Academic Press. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>